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Mathematical consequences of using various empirical expressions of crop yield as a function of temperature

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Abstract

Different expressions for the sensitivity of crops to temperature are commonplace. Sometimes absolute values in $t\ ha^{-1}\ {}^{\circ}C^{-1}$ are quoted and sometimes relative values expressed as $\%\ {}^{\circ}C^{-1}$. Values for the sensitivity are often calculated from curves fitted statistically to the data for yield and temperature. Mechanistic models of crop growth were built to avoid the difficulties of assessing the effects on yield of environmental variables that are often correlated with each other. Choosing an arbitrary mathematical relationship between yield and temperature can have bizarre implications for the expressions of temperature sensitivity; especially if the temperature range is small and the relationship is applied outside the range of data. We used a very simple analysis to illustrate the consequences of choosing different ways of expressing the effect of temperature on crop yield. The analysis presented shows that in the mean daily temperature range 22–32 $^{\circ}C$, rice yields decline by $-0.6\ t\ ha^{-1}\ {}^{\circ}C^{-1}$.
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1. Introduction

Intercepted solar radiation is the main determinant of crop growth (Monteith, 1977) but temperature, acting through many processes of plant growth, plays a role in controlling how much radiation is intercepted and how effectively it is used. The effects of temperature in biology have long been a source of confusion and controversy (Thornley and Johnson, 1990) and continue to be so. The effects on yield are more difficult to describe than those of radiation, because not all of the yield-shaping processes respond to temperature identically (Loomis and Connor, 1992; Paulsen, 1994). Mechanistic models describe individual processes in terms of temperature and other environmental factors; as a consequence the effects of temperature on yield can be obscured. Empirical equations are often used to describe a direct and transparent link between yield and temperature, but are vulnerable to error precisely because

they can appear not to take account of other environmental factors. In addition, the mathematical consequences of choosing a particular expression are often overlooked and we address that problem in this paper.

Often the word temperature is used in a very general way so that a reader may be uncertain what temperature is being described. At a given air temperature, a crop experiences a range of temperatures and those temperatures change throughout a day and over a growing season (Monteith, 1973; Peacock, 1975). Measurements of air temperature recorded at a meteorological station in a Stevenson screen are often used to describe the temperatures that crops experience and the average of daily maximum and minimum values is taken as the mean daily temperature. Moreover, the temperature may be an average for the year, for the growing season (a period within which crops are grown but not necessarily present for the whole of the season), for the growth duration of the crop, or for some specified period in the growth duration such as flowering. It is not our purpose to explore the definitions of temperature so to make progress we assume that the relevant temperature has been measured.

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There are crop-specific upper and lower limits of temperature beyond which yields are zero and in rice, as in many other crops, the effect of temperature on yield is non-linear (Loomis and Connor, 1992). Over a narrow range of temperatures, approximations are useful to describe the effects of temperature on yield, as a response curve. However, choosing a particular approximation commits the user to other temperature relationships, especially measures of change of yield with temperature that are implied by the choice of response curve. Those implications are often apparent when correlation is used to describe the temperature sensitivities of crops (Lobell and Asner, 2003; Peng et al., 2004).

The third assessment report (TAR) of the Intergovernmental Panel on Climate Change (IPCC, 2001) forecasts that by 2100 mean planet-wide surface temperatures will rise by 1.4–5.8 °C. There is evidence that night temperature is the cause of increases in global mean temperatures since the middle of the 20th century (Kukla and Karl, 1993). Between 1979 and 2003, minimum temperatures of the wet season and the dry season at IRRI increased at approximately 0.04 °C year^{-1}, which is 1 °C in 25 years (Sheehy et al., 2005). Establishing relationships between yield and temperature is important in the context of trying to understand the consequences of climate change. Unfortunately, there is a temptation to extrapolate relationships beyond the temperature range for which they were constructed. Allowing for that tendency should influence the choice of mathematical relationship to describe the response of yield to temperature.

In this paper, we explore the consequences of: (1) a constant absolute decline in yield with increasing temperature, (2) a constant relative decline (e.g. percentage) in yield with increasing temperature, (3) a quadratic equation used to describe the relationship between yield and temperature and (4) a logistic equation used to describe the relationship between yield and temperature. We illustrate the consequences for rice across the temperature range 16–42 °C using the data of Horie et al. (1995) and Baker and Allen (1993).

2. Methods: the response of grain yield (Y) to temperature (T)

2.1. Definitions

Temperature (T) will refer to air temperature unless stated otherwise. The absolute sensitivity of yield to temperature, $\alpha(T)$, is the change in yield caused by a change in temperature (dY/dT), when all other environmental variables are assumed to be constant or to have no effect on yield; the units are t ha^{-1} °C^{-1}. The relative sensitivity of yield to temperature, $\beta(T)$, is $\alpha(T)$ divided by the yield at that temperature ($1/Y \, dY/dT$); the units are °C^{-1}, but it is most often expressed as a percentage: % °C^{-1}. Throughout this paper, grain yield is given at 14% moisture content, the standard basis.

2.2. Case 1: α(T) is constant

If $\alpha(T)$ is constant and equal to a_1, we can write:

$$\frac{dY}{dT} = a_1 \tag{1}$$

and the relationship between yield and temperature is a straight line (by integrating Eq. (1)) and can be written as:

$$Y = a_1 T + b_1. \tag{2}$$

Then $\beta(T)$ is

$$\frac{1}{Y}\frac{dY}{dT} = \frac{a_1}{a_1 T + b_1}, \tag{3}$$

which is not constant but varies with temperature.

2.3. Case 2: β(T) is constant

If $\beta(T)$ is constant and equal to a_2 we can write:

$$\frac{1}{Y}\frac{dY}{dT} = a_2, \tag{4}$$

so that the $\alpha(T)$ is written as:

$$\frac{dY}{dT} = a_2 Y. \tag{5}$$

By integrating Eq. (5) we obtain

$$Y = Y_0 \exp[a_2(T - T_0)] \tag{6}$$

where Y_0 is the yield at temperature T_0.

2.4. Case 3: Quadratic equation describing the dependence of yield on temperature

A quadratic equation can be used to relate the data for yield and temperature:

$$Y = a_3 T^2 + b_3 T + c_3 \tag{7}$$

so that $\alpha(T)$ is

$$\frac{dY}{dT} = 2a_3 T + b_3, \tag{8}$$

and $\beta(T)$ is

$$\frac{1}{Y}\frac{dY}{dT} = \frac{2a_3 T + b_3}{a_3 T^2 + b_3 T + c_3}. \tag{9}$$

2.5. Case 4: Logistic describing the dependence of yield on temperature

Unlike the previous cases, the logistic description appears to be suited only for the initial and final parts of the temperature range, i.e. for growth in the ranges 16–22 and 32–42 °C. If the initial relative change in yield with temperature is proportional to a constant, but slows with increasing temperature towards an asymptotic value of

yield, Y_m, determined by factors other than temperature, we can write $\beta(T)$ as:

$$\frac{1}{Y} = \frac{dY}{dT} = a_4\left(1 - \frac{Y}{Y_m}\right), \tag{10}$$

where a_4 is an empirically determined temperature coefficient of yield, with units $^\circ C^{-1}$. At low values of Y, a_4 is equivalent to the relative temperature sensitivity of yield. We can write $\alpha(T)$ as:

$$\frac{dY}{dT} = a_4 Y\left(\frac{1 - Y}{Y_m}\right), \tag{11}$$

which on integration gives the relationship between yield and temperature as:

$$Y = \frac{Y_m}{1 + \exp[-a_4(T - b_4)]}, \tag{12}$$

where $T = b_4$ when $Y = Y_m/2$ and the maximum of $dY/dT = a_4 Y_m/4$ at $T = b_4$.

3. Results

We illustrate the first three cases for the temperature range 22–32 $^\circ C$. The equations above are in general form, so that where yield declines as temperature increases the signs of the parameter values will be such as to give negative values to $\alpha(T)$ and $\beta(T)$.

3.1. Case 1

Yoshida and Parao (1976) observed that at a given total of incident solar radiation received, rice yield declined with increasing mean daily temperature for the 25 days before flowering. Here, we re-calculate their parameters for the modern cultivar IR72 (Sheehy et al., 2001) and a constant daily solar radiation of 19.5 MJ m^{-2} (the average at the time of flowering in the dry season at IRRI). The yield equation can be written in the form of Eq. (2) as:

$$Y = 23.4 - 0.58T, \tag{13}$$

where $\alpha(T)$ is constant (a_1) with a value of -0.58 t ha^{-1} $^\circ C^{-1}$ (Fig. 1B) and the value of b_1 is 23.4 t ha^{-1}. Eq. (13) predicts that the yield between 22 and 32 $^\circ C$ declines linearly from 10.6 to 4.8 t ha^{-1} (Fig. 1A), whereas the relative temperature sensitivity of yield ($\beta(T)$) is non-linear and ranges from -5.5 to -12.0% $^\circ C^{-1}$ (Fig. 1C).

More recent data are available from experiments of Baker and Allen (1993). We constructed a linear regression using the data for yield and mean daily temperature, averaged over the crop growth duration, at a CO_2 concentration of 330 μmol mol^{-1} and obtained $Y = 22.7 - 0.57T$ ($P < 0.01$). At a CO_2 concentration of 660 μmol mol^{-1} the linear regression was $Y = 24.9 - 0.59T$ ($P < 0.05$).

3.2. Case 2

Values for $\beta(T)$ of about -5% $^\circ C^{-1}$ have been reported for mean daily temperature data of wheat, maize and rice (Brown and Rosenberg, 1997; Matthews et al., 1995) and we use that value here (Fig. 1F). In solving the simple differential equation and to be consistent with Case 1, we assume Y_0 is 10.6 t ha^{-1} and T_0 is 22 $^\circ C$ in Eq. (6), so that the relationship between yield and mean daily temperature is:

$$Y = 10.6\exp[-0.05(T - 22)]. \tag{14}$$

Between mean daily temperatures of 22 and 32 $^\circ C$, predicted yield declines from 10.6 to 6.4 t ha^{-1} (Fig. 1D); $\alpha(T)$ can be written as:

$$\frac{dY}{dT} = -0.05Y, \tag{15}$$

and it changes from -0.53 t ha^{-1} $^\circ C^{-1}$ at 22 $^\circ C$ to -0.32 t ha^{-1} $^\circ C^{-1}$ at 32 $^\circ C$ (Fig. 1E).

Peng et al. (2004) reported that $\beta(T)$ was -15% $^\circ C^{-1}$ (mean daily temperatures averaged over the crop duration) (Fig. 1F). The consequences of using that value ($\beta(T) = -15\%$ $^\circ C^{-1}$) are that between 22 and 32 $^\circ C$ predicted yields would decline from 10.6 to 2.4 t ha^{-1} (Fig. 1D). Values of $\alpha(T)$ would run from -1.59 t ha^{-1} $^\circ C^{-1}$ at 22 $^\circ C$ to -0.35 t ha^{-1} $^\circ C^{-1}$ at 32 $^\circ C$ (Fig. 1E).

3.3. Case 3

Peng et al. (2004) described the relationship between rice yield and mean daily minimum temperature during the growth duration for 12 consecutive years (dry seasons) in which mean daily minimum temperature varied between 22.1 and 23.7 $^\circ C$. They fitted a quadratic equation (published as $Y = -0.89T^2 + 39.2T - 423.6$) which gives positive yields for temperatures between 19.02 and 25.03 $^\circ C$ (Fig. 1G). Restricting interest to only 22–25 $^\circ C$, $\alpha(T)$ ranged from 0.04 to -5.3 t ha $^\circ C^{-1}$ (Fig. 1H) and $\beta(T)$ ranged from 0.49 to -3533% $^\circ C^{-1}$ (Fig. 1I) with a singularity at zero yield (relative change of minus infinity). In the range of mean daily minimum temperature actually recorded, $\beta(T)$ takes values from -1.7 to -59.3% $^\circ C^{-1}$. Note: it is probable that the quadratic equation has round-off errors in the coefficients and this can cause difficulties when comparing predictions with the data published by Peng et al. (2004).

3.4. Case 4A: Yield for mean daily temperature range 16–22 $^\circ C$

A logistic temperature response curve, closely resembling that of Horie et al. (1995) for 16–22 $^\circ C$ mean daily temperature, can be constructed using Eq. (12) with $Y_m = 10.75$ t ha^{-1}, $b_4 = 20$ $^\circ C$ and the empirical yield temperature coefficient $a_4 = 2$ $^\circ C^{-1}$. This value for max-
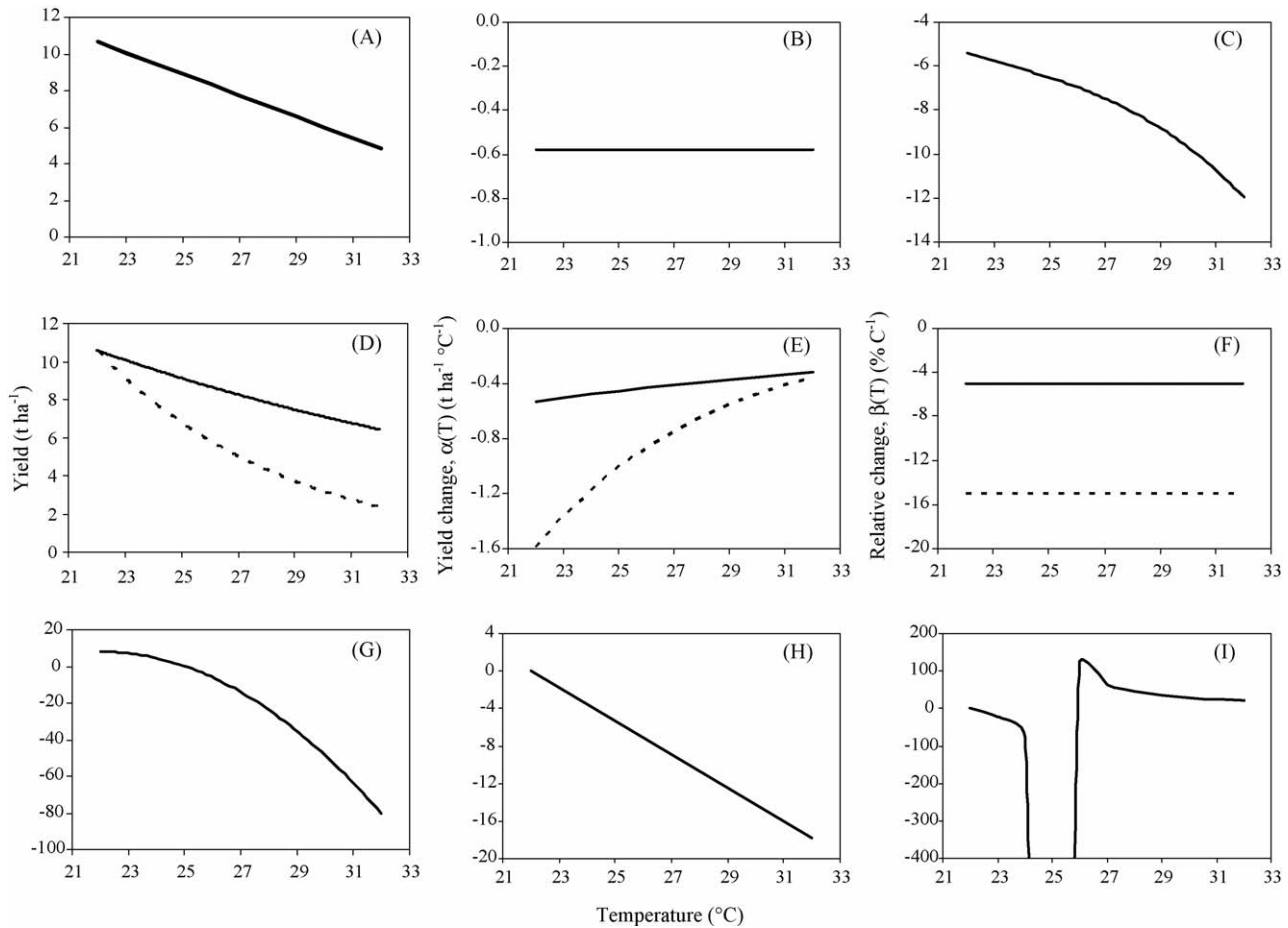
Fig. 1. The relationships between yield and daily mean temperature for rice in the range 22–32 °C with different initial assumptions. There are three related groups of graphs: A–C (Case 1) have constant change in yield for unit change in temperature (shown in graph B); D–F (Case 2) have constant relative change in yield with temperature (shown in graph F); and G, H and I (Case 3) have a quadratic equation for the response curve of yield on temperature (shown in graph G). Graphs A, D and G are response curves for yield and temperature, B, E and H are absolute yield change with temperature and C, F and I are relative yield change with temperature. In D, E and F the solid lines represent a relative change in yield of −5% °C^{-1} and the dashed lines a relative change in yield of −15% °C^{-1}. See text for other details of equations and sources of values for the parameters.

imum yield assumes average daily solar radiation of 20 MJ m^{-2}; yield is effectively zero at 16 °C and reaches a yield of 10.6 t ha^{-1} at 22 °C. The maximum value of $\alpha(T)$ is 5.4 t ha^{-1} °C^{-1} at 20 °C (Fig. 2B) and $\beta(T)$ shows a logistic pattern with values close to 200% °C^{-1} up to 18 °C and less than 3.6% °C^{-1} at temperatures greater than 22 °C (Fig. 2C).

3.5. Case 4B: Yield for temperature range 32–42 °C

In this temperature range, the data of Horie et al. (1995) suggests that yield declines logistically. To be consistent with the data of Yoshida and Parao (1976) in Case 1, in which the yield was 4.8 t ha^{-1} at a daily mean temperature of 32 °C, Eq. (12) can be written as:

$$Y = \frac{5.0}{(1 + \exp[1.3(T - 34.5)])}, \tag{16}$$

where Y_m is 5.0 t ha^{-1}, $b_4 = 34.5$ °C and a_4 is −1.3 °C^{-1}. The pattern of the decline in yield with temperature in this range largely reflects the relationship between fractional spikelet sterility and mean daily maximum temperature described by Horie et al. (1995).

Then the absolute sensitivity of yield to daily mean maximum temperature, $\alpha(T)$, is:

$$\alpha(T) = \frac{dY}{dT} = -1.3Y\left(\frac{1 - Y}{5.0}\right), \tag{17}$$

and $\alpha(T)$ reaches a minimum of −1.6 t ha^{-1} °C^{-1} at 34.5 °C as shown in Fig. 2E. Similarly, $\beta(T)$ can be written

$$\beta(T) = \frac{1}{Y}\frac{dY}{dT} = -1.3\left(\frac{1 - Y}{5.0}\right), \tag{18}$$

which is also a logistic function with values of $\beta(T)$ ranging from −4.9% °C^{-1} at 32 °C to −130% °C^{-1} at 42 °C (Fig. 2F).
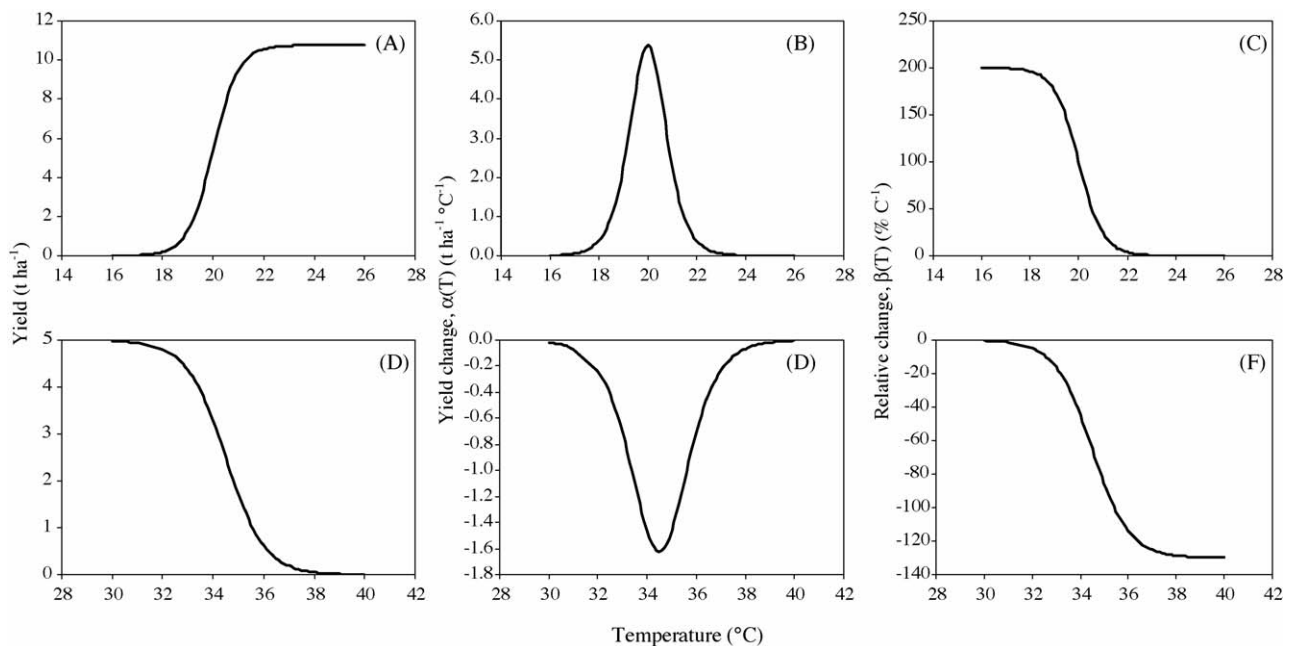
Fig. 2. The relationships between yield and temperature for rice as logistic curves in the ranges 16–22 °C (graphs A–C, yield increasing with daily mean temperature; Case 4A) and 32–42 °C (graphs D–F, yield decreasing with daily mean temperature; Case 4B). Graphs A and D are logistic response curves of yield and temperature, graphs B and E are absolute yield change with temperature and graphs C and F are relative yield change with temperature. See text for details of equations and sources of values for the parameters.

4. Discussion

The relationship between yield and temperature ($Y = f(T)$, the response curve), the absolute sensitivity of yield with temperature (dY/dT) and the relative sensitivity of yield with temperature ($1/Y\,(dY/dT)$) must be mathematically consistent. Starting with simple examples of the response curve, absolute change and relative change, we derived the mathematical implications for the other measures.

A constant negative value of $\alpha(T)$ (Case 1) implies that the relative severity of temperature damage increases with temperatures (Fig. 1A–C). In contrast, a constant negative value of $\beta(T)$ with increasing temperature (Case 2) implies that initially the crop is very sensitive to temperature damage, but it becomes less sensitive with increasing temperature (Fig. 1D–F). If the value of $\beta(T)$ was $15\%\,°C^{-1}$, as reported by Peng et al. (2004), then over the temperature range 22–32 °C the yields would decrease from 10.6 to 2.4 t ha^{-1} (Fig. 1D). In contrast, the experimental data of Baker and Allen (1993) suggests he yields would fall from 10.3 to 4.6 t ha^{-1}. Perhaps the range of mean daily temperatures (25.9–27.7 °C) observed by Peng et al. (2004) was too small to determine a temperature sensitivity with any degree of confidence, especially when other environmental factors were varying.

When a quadratic equation is used to describe a decrease in yield with increasing temperature (Case 3, Fig. 1G), it implies that the damaging effects of temperature increase

rapidly in a linear manner (Fig. 1H). However, nonsensical predictions of the effects of temperature can be made just outside the observed temperature range (Fig. 1G and I). Even within the recorded range of minimum temperature (1.6 °C) of Peng et al. (2004), $\beta(T)$ changes 32-fold. Their single figure summary of $-10\%\,°C^{-1}$ occurs at a minimum temperature of 22.46 °C and the value at the middle of their temperature range (22.9 °C) is $-21\%\,°C^{-1}$. The damaging effects of temperature may often increase rapidly with temperature, but using a quadratic equation to describe the response of a crop to temperature requires caution.

The use of a logistic relationship to describe the change in yield with temperature results in the absolute temperature response, $\alpha(T)$, having the same value at two different temperatures; one as the change in yield accelerates and the other as it decelerates (Fig. 2B and E). The only unique value of $\alpha(T)$ occurs at the point of transition between those two phases in the response of yield to temperature. The relative response to temperature, $\beta(T)$, also follows a logistic pattern (Fig. 2C and F).

Johnson and Thornley (1985) discussed a conceptual basis for considering the influence of temperature on plant and crop processes. However, yield is the consequence of integrating many temperature-dependent processes from germination to maturity. Temperature can affect differently the rates of acquisition of resources, the loss of resources, the efficiency with which acquired resources are transformed into products and it can damage mechanisms essential for the production of grains, e.g. floret sterility.

Perhaps the effects of temperature on yield can only be determined accurately using a mechanistic model, one that uses the quantitative relationships between each of the yield-shaping processes and temperature. But there are many gaps in the quantification of such relationships, e.g. effects of respiration on the reproductive mechanisms in rice and uncertainty concerning the appropriate values of such coefficients for field crops (Frantz et al., 2004; Mitchell et al., 1991). Approximate descriptions of the effects of temperature on yield over narrow temperature ranges are likely to remain useful, bringing with them the temptations of extrapolation and inconsistency. In particular, where change is expressed as a percentage per degree ($\beta(T)$), the default interpretation is Case 2, constant relative change (Fig. 1F) implying an exponential response curve of yield with temperature (Fig. 1D). If this not intended, then the change must be expressed relative to a base yield and temperature which should be clearly stated.

The remarkably similar yield-temperature responses observed by Yoshida and Parao (1976) and Baker and Allen (1993) indicates that $\alpha(T)$ may be constant for rice in the temperature range 22–32 °C. Their results showed that rice yields decrease by approximately -0.6 t ha^{-1} °C^{-1} (and increase by about 0.5 t ha^{-1} for every 75 μmol mol^{-1} increase in CO_2 concentration). As always, using linear descriptions (Case 1) of the effects of temperature over small temperature ranges is the easiest and simplest approach to describing the effects of temperature on complex systems. In the absence of a detailed understanding of the system's behavior, it is the approach least likely to cause unexpected problems.

5. Conclusions

If the absolute response to temperature is assumed to be constant, because the relationship between yield and temperature is a straight line, then the relative response is a polynomial curve. If the relative response to temperature is constant, then the relationship between yield and temperature must be exponential and the absolute response is a function of yield. Choosing an arbitrary mathematical relationship, such as a quadratic, for the relationship between yield and temperature can have bizarre implications for the expressions of temperature sensitivity; especially if the temperature range is small and the relationship is applied outside the range of data. Logistic curves relating yield to temperature produce measures of absolute and relative change that appear strange at first but are interpretable.

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